Zoosyst. Evol. 101 (4) 2025, 1613–1620 | DOI 10.3897/zse.101.166584

Gibbosula sinensis, a new species on the verge of extinction of the world's most threatened freshwater mussel family Margaritiferidae Henderson, 1929 from China (Bivalvia, Palaeoheterodonta, Unionida)

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Academic editor: Le-Jia Zhang ♦ **Received** 25 July 2025 ♦ **Accepted** 5 August 2025 ♦ **Published** 26 August 2025

Abstract

A new species of freshwater mussel, *Gibbosula sinensis* Z.-G. Chen, Y.-T. Dai, H. Chen & X.-P. Wu, **sp. nov.**, is described from the lower Lancangjiang River Basin in Yunnan, China based on comparative morphology and molecular phylogeny. The new species can be distinguished from congeners by the oblong, slender, very curved, relatively thin, fragile, and rather smooth shell, the front end of the shell higher than the posterior end, and the special habitat selection. The new species is on the verge of extinction and urgently requires attention and protection.

Key Words

Biodiversity, molluscs, phylogeny, taxonomy

Introduction

Margaritiferidae Henderson, 1929, is a group of medium to large freshwater mussels widely distributed across North America, Europe, North Africa and Asia (Bolotov et al. 2016; Araujo et al. 2017; Lopes-Lima et al. 2018; Graf and Cummings 2025; MolluscaBase 2025). Compared to its wide distribution, the species diversity of the family is relatively limited, encompassing only four genera and 15 extant species (Bogan and Do 2016; Lopes-Lima et al. 2018; Wu et al. 2020; Graf and Cummings 2025; MolluscaBase 2025). The family is the most threatened freshwater mussel worldwide, with all species assessed with sufficient data presenting a near threatened or threatened conservation status (Lopes-Lima et al. 2018). In China, only five extant species of the family have been recorded: *Margaritifera dahurica* (Middendorff, 1850), *Gibbosula confragosa* Frierson, 1928, *G. crassa* (Wood, 1815), *G. laosensis* (Lea, 1863), and *G. rochechouartii* (Heude, 1875) (He and Zhuang 2013; Wu et al. 2020; Guo 2022; Graf and Cummings 2025; MolluscaBase 2025). The distribution of these species encompasses the substantial expanse of the eastern Chinese mainland, extending from the Heilongjiang River Basin at the northernmost reaches to the Pearl River and Lancangjiang River Basins at the southernmost limits (He and Zhuang 2013; Guo 2022).

Based on the specimens collected from the Lancangjiang River Basin (Mekong) in Xishuangbanna, Yunnan, China in 2023–2025, we describe a new species of *Gibbosula* Simpson, 1900. The discovery enhances the

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diversity of freshwater mussels in China and underscores the imperative for the conservation of the extremely threatened family Margaritiferidae.

Materials and methods

Specimens were collected from Yunnan of China in 2023–2025. Specimens for molecular phylogenetic analysis were initially frozen at -20 °C for 24 hours and subsequently thawed at room temperature for 8 hours to take out the soft parts. The soft parts were then fixed in 95% ethanol. Empty shells were cleaned, dried, and preserved at room temperature. Eight specimens were fixed in 8% formalin to observe the morphology of the soft part. Photographs were taken by camera and edited in Adobe Photoshop CC 2015 (Adobe, San Jose, USA). Maps were made in ArcGIS Pro (Esri, Redlands, USA).

Genomic DNA was extracted from foot tissues preserved in 95% ethanol using a TIANamp Marine Animals DNA Kit (Tiangen Biotech, China). The quality and concentration of the DNA were checked on 1% agarose gel electrophoresis and NanoDrop 2000 (Thermo Scientific, USA). Partial cytochrome c oxidase subunit 1 (*COI*) was amplified and sequenced for molecular phylogenetic analyses. Polymerase chain reaction (PCR) systems, conditions and primer pairs were followed Chen et al. (2023). The *COI* sequences were aligned using MEGA v. 6.0 (Tamura et al. 2013). The accession numbers of all sequences used in this study are given in Table 1.

Phylogenies reconstructed by the *COI* sequences using Maximum Likelihood (ML) and Bayesian Inference (BI). Family Trigoniidae Lamarck, 1819 of order Trigoniida and five families of order Unionida, Unionidae Rafinesque, 1820, Mulleriidae Deshayes, 1832, Etheriidae Deshayes, 1832, Iridinidae Swainson, 1840, and Hyriidae Swainson, 1840 were used as the outgroups for rooting the trees. The best-fit model for each gene and gene partition was calculated by PartitionFinder2 v. 1.1 (Lanfear et al. 2017), based on the corrected Akaike Information Criterion (AICc) and using a heuristic search algorithm. The program proposed the division of the concatenated dataset into two partitions, comprising partitions for the first and second codon positions of the *COI* gene and the third codon positions of the *COI* gene. The best-fit model was determined to be GTR+I+G for the first and second codon positions of *COI*, while GTR+G was selected for the third position of *COI*. ML analyses were performed in IQ-TREE v. 1.6.12 (Minh et al. 2013) using the Ultrafast bootstrap approach (Minh et al. 2013) with 10,000 iterations. Bayesian inference (BI) analysis was conducted in MrBayes v. 3.2.6 (Ronquist et al. 2012). Four simultaneous runs with four independent Markov Chain Monte Carlo (MCMC) were implemented for 10 million generations, and trees were sampled every 10,000 generations

Table 1. Genbank accession numbers of sequences used in this study.

Species	Accession number	Locality
Margaritiferidae		
Gibbosula sinensis sp. nov. 1	PX067295	Nanbanhe River, Xishuangbanna, Yunnan, China
Gibbosula sinensis sp. nov. 2	PX067296	Nanbanhe River, Xishuangbanna, Yunnan, China
Gibbosula sinensis sp. nov. 3	PX067297	Nanbanhe River, Xishuangbanna, Yunnan, China
Gibbosula sinensis sp. nov. 4	PX067298	Nanbanhe River, Xishuangbanna, Yunnan, China
Gibbosula sinensis sp. nov. 5	PX067299	Nanbanhe River, Xishuangbanna, Yunnan, China
Gibbosula sinensis sp. nov. 6	PX067300	Nanbanhe River, Xishuangbanna, Yunnan, China
Gibbosula laosensis 1	KR006698	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 2	KR006699	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 3	KP843087	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 4	JX497731	Nam Long River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 5	JX497732	Nam Long River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 6	JX497733	Nam Long River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 7	KJ943551	Nam Long River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 8	KJ943552	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 9	KJ161531	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 10	KJ161532	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 11	KJ161533	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 12	KJ943553	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 13	KJ943554	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 14	KJ943555	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 15	KU763224	Mun River, Thailand
Gibbosula laosensis 16	KU763225	Luang Prabang, Laos
Gibbosula laosensis 17	KU763226	Luang Prabang, Laos
Gibbosula laosensis 18	JX497734	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos
Gibbosula laosensis 19	JX497735	Nam Pe River, Nam Ou River Basin, Phongsali Province, Northern Laos

Species	Accession number	Locality
Gibbosula crassa 1	MH293546	Bang River, Cao Bang, Vietnam
Gibbosula crassa 2	MH293547	Bang River, Cao Bang, Vietnam
Gibbosula rochechouartii 1	MF072498	Poyang Lake, Yangtze, China
Gibbosula rochechouartii 2	MF072502	Poyang Lake, Yangtze, China
Cumberlandia monodonta 1	AY579131	Missouri, USA
Cumberlandia monodonta 2	MH293545	Meramec River, Missouri, USA
Margaritifera dahurica 1	KJ161516	Ilistaya River, Primorye, Russia
Margaritifera dahurica 2	KJ161520	Ilistaya River, Primorye, Russia
Margaritifera falcata 1	AY579128	Idaho, USA
Margaritifera falcata 2	AY579127	North Umpqua River, Oregon, USA
Margaritifera hembeli 1	KU763218	Valentine Creek, Louisiana, USA
Margaritifera hembeli 2	KU763219	Brown Creek, Louisiana, USA
Margaritifera laevis	KU763222	Iwaizumi, Honshu, Japan
Margaritifera margaritifera 1	KU763227	Locust Creek, Pennsylvania, USA
Margaritifera margaritifera 2	AF303342	Nore River, Ireland
Margaritifera marrianae	KU763243	Hunter Creek, Alabama, USA
Margaritifera middendorffi 1	AY579124	Iturup, Kuril Islands, Russia
Margaritifera middendorffi 2	KJ161547	Nachilova River, Kamchatka, Russia
Pseudunio auricularius 1	AY579125	Ebro River, Tarragona, Spain
Pseudunio auricularius 2	AF303309	Canal Imperial, Zaragoza, Spain
Pseudunio homsensis	KX550090	Karasu River, Turkey
Pseudunio marocanus 1	EU429678	Oum Er Rbia River, Morocco
Pseudunio marocanus 2	EU429679	Laabid River, Morocco
Unionidae		
Lampsilis cardium	KX713472	Illinois, USA
Potomida littoralis	KP217871	Cadiz, Spain
Hyriidae		
Hyridella australis	KX713467	New South Wales, Australia
Triplodon corrugatus	KX713505	Peru
Mulleriidae		
Anodontites elongata	KX713444	Peru
Lamproscapha ensiformis	KX713471	Peru
Etheriidae		
Etheria elliptica	KX713462	Zambia
Iridinidae		
Aspatharia pfeiffieriana	KC429107	Chambeshi River, Zambia
Chambardia wahlbergi	KX713448	Zambia
Trigoniidae		
Neotrigonia lamarckii	KC429105	North Stradbroke Island, Australia
Neotrigonia margaritacea	U56850	Tasmania, Australia

with a burn-in of 25%. The convergence was checked with the average standard deviation of split frequencies <0.01 and the potential scale reduction factor (PSRF) ~ 1. Trees were visualized in FigTree v.1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/).

Abbreviations. NCUMB: Museum of Biology, Nanchang University (Nanchang, Jiangxi, China); ZMNH: Zhejiang Museum of Natural History (Hangzhou, Zhejiang, China); USNM: National Museum of Natural History, USA (Washington, D.C., USA); aam: anterior adductor muscle; pam: posterior adductor muscle; ea: excurrent aperture; ia: incurrent aperture; pia: papillae of the incurrent aperture; pea: papillae of the excurrent aperture; ig: inner gills; og: outer gills; m: mantle; lp: labial palps; vm: visceral mass; f: foot.

Results

Phylogenetic analyses

The sequence dataset consisting of 59 *COI* sequences from 26 species, including with 11 outgroup taxa, was employed for phylogenetic analyses (Table 1). The alignments of *COI* genes had a length of 656 characters. Within the alignment, 315 sites were variable, and 283 sites were parsimony informative. The Bayesian and Maximum Likelihood analyses produced almost same phylogenies (Fig. 1). The new species represents a sister but divergent lineage to *Gibbosula laosensis*, although with moderate support (BS/PP = 83/0.83). The p-distances of *COI* sequences between the new species and its congeners is 12.1%–14.8%.

Figure 1. Maximum Likelihood tree and Bayesian inference tree inferred from *COI* gene sequences. Bootstrap supports/posterior probabilities are shown on the left/right of nodes on the tree if greater than 50%.

Systematics

Family Margaritiferidae Henderson, 1929
Subfamily Gibbosulinae Bogan, Bolotov, Froufe & Lopes-Lima, 2018

Genus *Gibbosula* Simpson, 1900

Type species. *Mya crassa* Wood, 1815, by original designation.

Gibbosula sinensis Z.-G. Chen, Y.-T. Dai, H. Chen & X.-P. Wu, sp. nov.

https://zoobank.org/A482FBB5-3619-45BC-B949-E37651EA97A4

Figs 2, 3, 5D

Gibbosula laosensis – Guo 2022: 42 (southern Yunnan).

Type material. ***Holotype*:** • NCUMB B2507001, Nanbanhe River, a large tributary of the Lancangjiang River [澜沧江支流南班河], upstream of Menglun Town [勐仑镇上游], Xishuangbanna Dai Autonomous Prefecture [西双版纳傣族自治州], Yunnan Province [云南省], China, leg. Z.-G. Chen, Y.-T. Dai, H.-F. Hu, Y.-Y. Zhang, March 2023.

***Paratypes*:** • 18 shells with soft part, 27 paired dead empty shells, 62 single piece dead empty shells. NCUMB B2507002–011 (soft part stored in alcohol separately), leg. Z.-G. Chen, March 2024, other information same as holotype; NCUMB B2507012–019 (soft part kept in shell and stored in formalin), NCUMB B2507020–045 (paired dead empty shells), ZMNH RS202501 (paired dead empty shell), NCUMB B2507047–104 (single piece dead empty shells), ZMNH RS202502–05 (single piece dead empty shells), other information same as holotype.

Diagnosis. Shell oblong, slender, very curved, relatively thin, fragile, rather smooth. Front end of the shell higher than the posterior end. Inhabiting the deep torrent of the wide section of the lower Lancangjiang River (upper Mekong River).

Description. Shell large, symmetric, flat, relatively thin, fragile, sub-glossy, oblong, slender, very curved,

rather smooth, dark brown to black. Anterior, dorsal and posterior margin rounded; ventral margin concave. Umbo smooth, inflated, slightly under hinge line, located at 1/4 of the dorsal margin, and often eroded. Umbo cavity shallow. Growth lines arranged in irregular concentric circles. Hinge long and strong. Mantle attachment scars small, deep and sparse. Mantle muscle scars obvious. Anterior adductor muscle scars irregular oval, deep and coarse; posterior adductor muscle scars oval, smooth. Left valve with two pseudocardinal teeth, anterior one reduced, posterior one strong and connected to lateral teeth; right valve with two pseudocardinal teeth, anterior one strong and high, posterior one reduced, connected to lateral teeth. Lateral teeth of both valves relatively strong, rough, long and thick. Nacre white, with irregular yellow halo in partial individuals.

Mantle light brown. aperture margins black, papillae of the excurrent aperture highly degraded, papillae of the incurrent aperture strong and forked. Gills light brown, inner gills slightly longer and wider than outer gills. Labial palpsrown, irregular triangle, distally pointed. Visceral mass grayish white. Foot black, fades to brown in formalin.

Measurements. Holotype: shell length 116.4 mm, height 45.3 mm, width 30.4 mm. Paratypes: shell length 101.9–130.2 mm, height 40.3–49.1 mm, width 27.2–36.0 mm.

Etymology. The species is made from Latin *Sino* for China, referring to its type locality. The Chinese vernacular name is 中华弓背蚌 (pīnyīn: zhōng huá gōng bèi bàng) and the English vernacular name is Chinese freshwater pearl mussel.

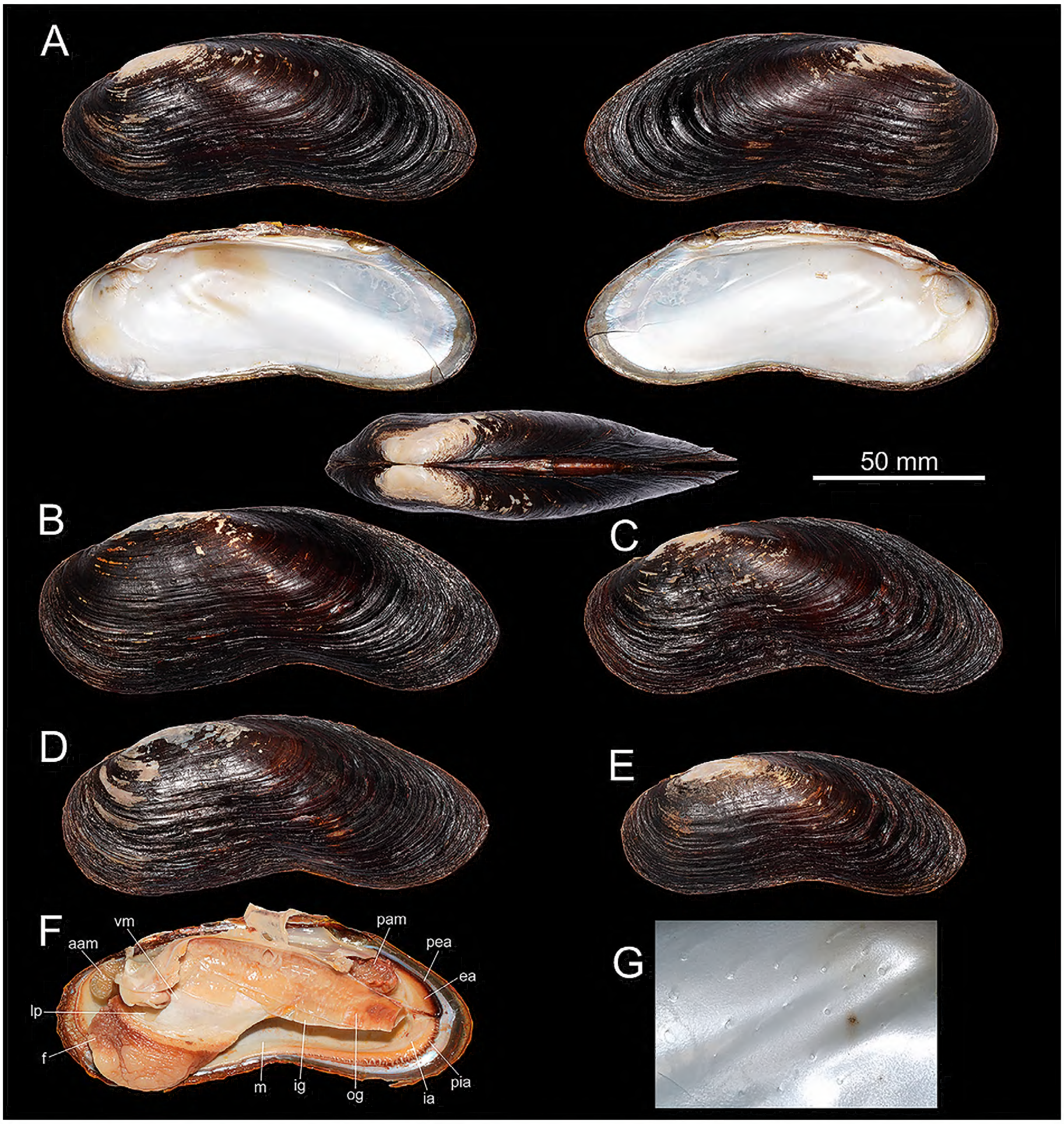

Figure 2. *Gibbosula sinensis* sp. nov. **A.** Holotype, NCUMB B2507001; **B–E.** Partial paratypes, NCUMB B2507002–05; **F.** Paratype, NCUMB B2507012, shows the soft anatomy; **G.** Shows mantle attachment scars.

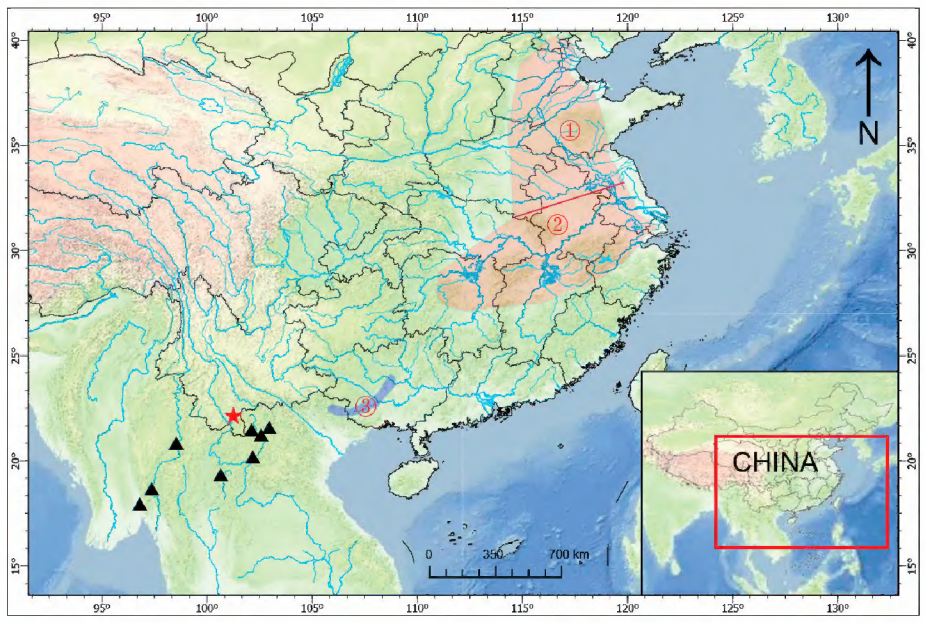

Figure 3. Distribution of genus *Gibbosula*. **1.** Historical distribution of *G. confragosa* and *G. rochechouartii*; **2.** Current distribution of *G. rochechouartii*; **3.** *G. crassa*; **star.** *Gibbosula sinensis* sp. nov.; **triangle.** *G. laosensis*.

Figure 4. The environment of the Nanbanhe River. **A.** Habitat of *Gibbosula sinensis* sp. nov.; **B.** The environment of river sections without *Gibbosula sinensis* sp. nov. habitat.

Distribution and ecology. Known from several kilometers of the Nanbanhe River upstream of Menglun Town (Fig. 3). Living under huge stone in the deep torrent of the wide river section (Fig. 4). The habitat will not be exposed out of the water even during the season with the lowest water level. Usually found together with *Lens comptus* (Deshayes, 1876), *Unionetta fabagina* (Deshayes, 1876), and *Bineurus mouhotii* (Lea, 1863). The population is extremely small, with fewer than 100 living animals found in a 3-year survey. The reproduction of the new species has encountered serious problems, the population is almost entirely composed of elderly individuals and with no juveniles. It will soon become extinct without protective measures.

Remarks. The new species was misidentified as *G. laosensis* by Guo (2022). Guo (2022) vaguely recorded the distribution of "*G. laosensis*" in China as southern Yunnan, which is actually the type locality of the new species.

Discussion

The placement of the new species within *Gibbosula* is supported by both its morphology and molecular phylogeny. Within the genus, the new species can be easily distinguished from *G. confragosa*, *G. crassa*, and *G. rochechouartii* by the oblong, slender, thin, fragile, and rather smooth shell (vs. irregular oval, fat, very thick and carved shell) (Fig. 5). The new species resembles *G. laosensis* on account of the similar shell shape, but differs by the more slender and more curved shell, the front end of the shell higher than the posterior end (vs. lower or equal), and the different habitat selection (deep torrent of the wide river section vs. shallow stream) (Bolotov et al. 2014). The molecular phylogenetic results also provide strong support for the independence of the new species. The new species exhibited significant genetic differentiation (12.1%) with *G. laosensis* from three localities in Laos and Thailand, indicating that it is an independent species rather than an upstream population of *G. laosensis*. The differentiation between these two species may be attributable to divergent habitat selection strategies.

A grave problem was identified concerning the reproductive capacity of the new species during the course of field surveys. The population was found to be predominantly composed of elderly individuals, with a complete absence of juveniles. In view of the fact that the population size is small and extremely threatened, and the economic value of the new species is high, the precise type locality will not be disclosed in this article until such time as further protective measures have been implemented. We take the congener also distributed in southern China, *G. crassa*, as an example. It has been subject to severe illegal fishing in recent years, with all living animals and even every empty shell in the Shuikouhe River being caught and sold. Despite the fact that *G. crassa* is classified as a national second-class protected animal in China, its shells are still being illegally traded on Chinese e-commerce platforms, such as Xianyu [闲鱼] (Suppl. material 1). The Chinese population of *G. crassa* is facing an imminent threat of extinction. Another congener, *G. confragosa*, which is distributed in northern China, is likely to have gone extinct earlier. This species has never been observed alive in the wild since its initial description. It is evident that the vast majority of the substantial rivers in the northern China have either desiccated or been transformed into reservoirs. This phenomenon renders

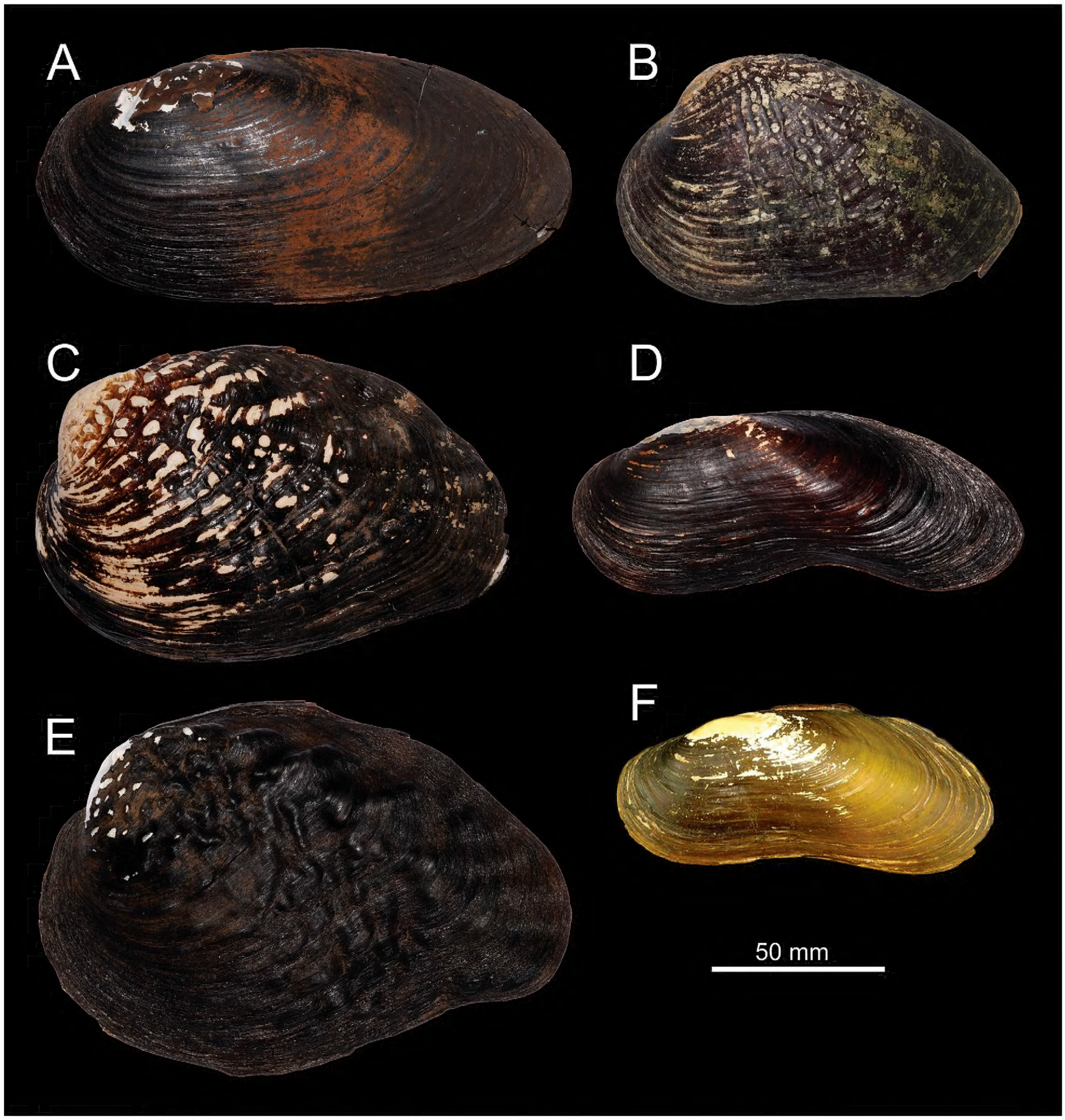

Figure 5. Morphological comparison of family Margaritiferidae distributed in China and *G. laosensis*. **A.** *Margaritifera dahurica*, Heihe, Heilongjiang, China; **B.** *Gibbosula crassa*, Shuikou, Chongzuo, Guangxi, China; **C.** *G. confragosa*, Baigou, Baoding, Hebei, China; **D.** *Gibbosula sinensis* sp. nov., Menglun, Xishuangbanna, Yunnan, China; **E.** *G. rochechouartii*, Wucheng, Jiangxi, China; **F.** *G. laosensis*, holotype, USNM 86160, Laos Mountains, Graf and Cummings (2025).

it improbable for *Gibbosula* to subsist within the region, given its reliance on the flowing waters of these substantial rivers. Even *G. rochechouartii*, which exhibits the widest distribution and largest population in the genus, has experienced severe decline in its distribution range. The species became extinct in northern China along with *G. confragosa*, and the remaining population retreated to the middle and lower Changjiang River (Yangtze). As the most threatened freshwater mussel group of the world, the new species and its congeners require urgent attention and protection.

Acknowledgements

We thank Ivan N. Bolotov and Arthur E. Bogan for their valuable comments on the manuscript; subject editor Le-Jia Zhang for efficiently processing the manuscript; Jing-Xin Liu (Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences), Zhao-Peng Jing (Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences), Peng Zhang (Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences), Jiang-Bo

Zhao (Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences), Zhi-Xian Sun (Institute of Zoology, Chinese Academy of Sciences), Ren-Fei Ma (Hebei), Peng Wei (Tianjin), and Ying-Ying Zhang (Nanchang University) for assistance in collecting specimens. This study was supported by the National Natural Science Foundation of China under Grant No.32360132.

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Supplementary material 1

Illegal trade of *Gibbosula crassa* on Xianyu

Authors: Zhong-Guang Chen, Yu-Ting Dai, Hui Chen, Hong-Fei Hu, Jiao Jiang, Liang Guo, Shan Ouyang, Xing-Xing Zhao, Xiao-Ping Wu

Data type: jpg

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Link: https://doi.org/10.3897/zse.101.166584.suppl1